

June 1, 1899.

Professor T. G. BONNEY, Vice-President, in the Chair.

A List of the Presents received was laid on the table, and thanks ordered for them.

Professor Ludwig Boltzmann, Professor Anton Dohrn, Professor Emil Fischer, Dr. Georg Neumayer, and Dr. Melchior Treub, were balloted for and elected Foreign Members of the Society.

The following Papers were read:—

- I. "The Parent-rock of the Diamond in South Africa." By Professor T. G. BONNEY, F.R.S.
- II. "Experimental Contributions to the Theory of Heredity. A. Telegony." By Professor J. C. EWART, F.R.S.

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"The Characteristic of Nerve," By AUGUSTUS D. WALLER, M.D., F.R.S. Received February 3,—Read February 16, 1899.

The object of the present preliminary series of experiments was to determine whether the excitability (or, as I should prefer to say in this connection, the mobility) of living matter can be gauged by the rate of impact of a mobilising stimulus; in other words, whether, for various kinds of more or less mobile protoplasm, an optimum stimulation-gradient can be found, above and below which the curve of stimulation is less perfectly adapted to the movement caused by stimulation. In, *e.g.*, the case of the rolling of a ship, there is an optimum wave-length and wave-face outside the limits of which the "mobilisation" is less than maximal. And just as the optimum wave-length giving greatest movement by least energy harmonises with and gives therefore measure of the oscillation-period of a particular ship, so the optimum gradient of mobilising energy producing greatest excitation by least energy, might be expected to give measure of the excitation-period proper to a particular tissue, *and to characterise that tissue.*

The best instrument at our disposal for an examination of this point is obviously a condenser, of varied capacity, charged at varied pressure. This method of excitation has been put into effect by several previous observers. Chauveau(1) first systematically studied the "law of contractions," and demonstrated upon frog's nerve that the make

excitation is kathodic. Dubois (4, 5), of Bern, studied the law of contractions upon human nerve, and came to the conclusion that the greater and smaller effects of condenser discharges are governed by the greater and smaller *quantities* of electricity in play. Hoorweg (11, 12), Cybulsky and Zanietowsky (9, 10) studied the effects more closely upon frog's nerve; the first-named observer concluded that the effects are a function of *intensity*; while the last two observers, from very similar observations, concluded that the magnitude of excitation is a function of *energy*. Salomonsen (8), Boudet (2), and D'Arsonval (6, 7) come to the same conclusion, and the last-named observer makes use of an expression—"la caractéristique de l'excitation"—very similar to the designation that I had been independently led to adopt, in ignorance of its previous use in a different sense.

The problem is, I think, to be considered from the following *a priori* point of departure:—A stimulus arouses excitable matter by reason of its actual energy and not of its mere quantity. A weight *per se* is not a stimulus, but a weight dropped from a height acts as a stimulus that is to be expressed in terms of energy. One gram fallen through 1 cm. strikes and stimulates with an actual energy of 1000 (or more precisely 981) ergs. Similarly, as regards the electrical stimuli afforded by the (charge or) discharge of a condenser, it is neither the quantity (coulomb) nor the pressure (volt) that alone gives measure of the stimulus, but the energy (Joule or  $10^7$  ergs) of that quantity at that pressure. A nerve (or other excitable tissue) may be struck and stimulated by an electrical energy of so many ergs. And we are adequately acquainted with the physiological value of a stimulus when we know:—First, its absolute value in ergs or fraction of an erg. Second, the rate at which such energy impinges upon and sets in motion the excitable molecules under investigation.

The absolute value of a true minimal stimulus in ergs or fraction of an erg, is ascertained by determining the optimum capacity and voltage at which a minimal response is obtained. The energy  $E$  in ergs  $= 5 FV^2$ , where  $F$  is in microfarads and  $V$  in volts.

Its rate of impact depends upon the rate of (charge or) discharge  $= \frac{V}{FR} \times$  a constant, where  $R$  denotes the resistance in circuit in ohms, and can therefore be expressed by a number that will be higher or lower according as the rate of discharge is greater or smaller.\*

\* With the same units as above, and with the unit of time  $= 10^{-6}$  second, the constant is 0.8687. In the subjoined data it has been taken as 868700 for the unit of time  $= 1$  second.

For certain ends it is convenient to indicate the rate of discharge of energy by stating the time necessary for its fall to any given fraction  $1/n$  of its original value, according to the formula  $t = FR \frac{\log n}{2 \log e}$ ; *e.g.*, with a capacity of 0.01 microfarad,

The number of the true minimal stimulus at optimum capacity and voltage, is what I propose to designate as the characteristic, or otherwise stated—the characteristic is the constant of the curve of the smallest discharge of energy that can provoke movement, or of the discharge of energy provoking greatest movement.

By suitable adjustment of capacity and voltage we may obtain the discharge of any desired energy—at any desired rate, if we also know the resistance through which discharge is made. From a small condenser at high voltage, and from a large condenser at low voltage, we may obtain the discharge (of equal quantities or) of equal energies, but in the first case rapidly and in the second case slowly. We may so adjust capacity and voltage, as to deliver constant energy in a series of curves of varying steepness, and find by experiment the more or less precise limits of steepness between which the motion or excitation is greatest. The number denoting that steepness of energy discharge by which a nerve is most economically mobilised, signifies the optimum adaptation of excitation to excitability, and is its characteristic. At that number the nerve is excited by the minimum of energy. With a stimulus of higher or lower number, more energy is necessary to produce an equal effect.

Taking either a series of stimuli of given energy, but of varying gradients, as in experiments 1 and 9, we are to observe at what gradient the maximum effect is produced. Or as in experiment 2, making a series of trials with varying amounts of energy from varying capacity and voltage, we are to observe at what minimum energy discharge the smallest perceptible effect is produced, and thence calculate the characteristic.

And even without actually determining the characteristic by means of its upper and lower limits, we may often usefully ascertain whether it is above or below a lowest or highest constant at the end of a series of experimental data. Thus in experiment 6, a minimal energy has not been reached, and we cannot therefore say that the characteristic has been determined; we know however, that it is less than 10.4. In experiment 4 the characteristic, as defined above, has not been actually 11382 and 0.6 since the stimulus has not been truly minimal; but these values have been those of the constants of suitable stimuli not far from minimal, and we know therefore that the characteristic has been nearer to the higher value at high temperature, nearer to the lower value at low temperature.

a resistance of 100,000 ohms, and  $1/n = \frac{1}{4}$ , the time of discharge of  $\frac{2}{3}$  of the original energy is 0.000693 sec. If the voltage under which this discharge takes place is 0.2, the original energy is 0.002 erg, and the number indicating its rate of discharge is 174. If 0.01 mf. and 0.2 v. should be the optimum capacity and voltage of a minimal effect by excitation of a given nerve, *i.e.*, a true minimal or optimal minimal stimulus, then the number 174 is the characteristic of the nerve.

Strictly speaking, the term minimal stimulus in, *e.g.*, experiment 2, applies only to the two values 0.001134 erg and 0.002 erg in the two groups respectively, since in these two cases only is the energy of the stimulus at its minimum.

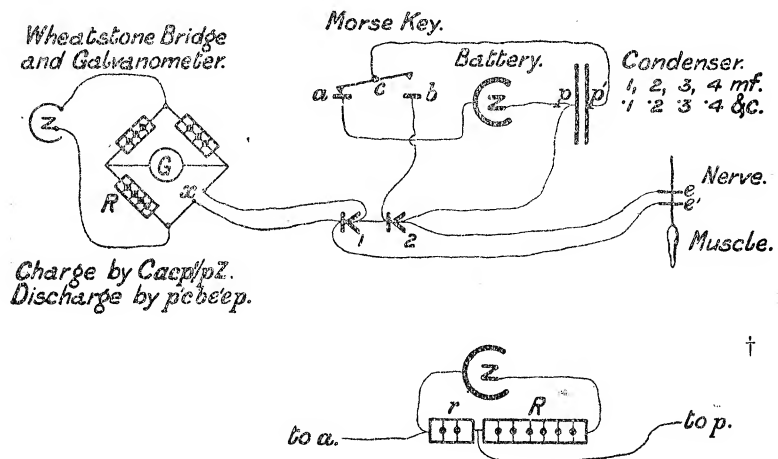
But in accordance with ordinary tests by induction currents, the term "minimal" is applied to stimuli that are certainly not of minimal energy, but that produce minimal effects. And in this loose sense all the trials of the above groups give minimals, in the first group minimals of effective capacity at the several voltages, in the second group minimals of effective voltage at the several capacities.

The ambiguity may be provisionally neutralised by making use of the expression "optimal minimal" for the true minimal stimulus *qua* its energy value, and by avoiding use of the term minimal for stimulation by induction shocks, or by condenser discharges of a gradient above or below the optimum or characteristic gradient.

The *method* followed will be most readily understood by consideration of the diagram.

(A) The apparatus for excitation, composed of battery, condenser, and a Morse key, is connected with the nerve of a nerve-muscle preparation by unpolarisable electrodes, the circuit being arranged so that charge of the condenser is at contact *a*, and does not traverse the nerve, while discharge is at contact *b*, and alone traverses the nerve. During excitation the key  $K_1$  is closed, and the key  $K_2$  open.

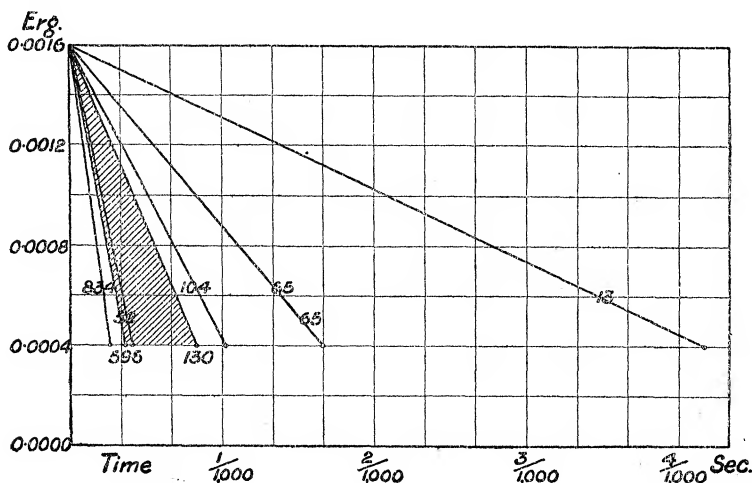
(B) The apparatus for measurement of resistance, composed of battery, Wheatstone bridge, and galvanometer, is connected with the nerve by opening the key  $K_1$  (and closing the key  $K_2$ ).



To obtain fractions of a volt the disposition figured in the smaller diagram † was adopted.

The muscular contraction was watched for, and occasionally recorded in the usual way.

As regards the human subject, the circuit was as before, a Stöhrer's battery up to 60 volts being used to charge the condenser. One large electrode (the "indifferent" electrode) was strapped to the abdomen; a second small electrode (the "testing" electrode) was fixed over an accessible nerve, such as the ulnar, median, or peroneal.



To illustrate rate of energy discharge and approximate gradients when the constant has not less than two digits nor more than three digits. The shaded area indicates range within which the nerve characteristic must have fallen.

The procedure was of three types:—(1) To take a series of combinations between voltage and capacity, so as to deliver constant energy at various rates; (2) to take a series of voltages and find for each voltage the smallest capacity at which contraction was visible; (3) to take a series of capacities and find for each capacity the smallest voltage at which contraction was visible.

The first plan has the considerable advantage of permitting the use of a myograph. It is chiefly serviceable for the purpose of a preliminary orientation, *i.e.*, when it is desired to find quickly the range at which the characteristic is to be looked for. Having obtained a minimal effect with any given voltage and capacity, the next test is to be made with half the voltage and four times the capacity, *i.e.*, with the same energy as before, but with that energy falling by a curve with a constant equal to one-eighth of the constant of the previous case. If the effect is manifestly greater, the voltage is again to be halved and the capacity quadrupled from the starting point of a new minimal effect. If, on the other hand, after the first step in reduction of the

constant, there is no effect at all, a test is taken in the opposite direction, with double the voltage and one-fourth the capacity, *i.e.*, with the constant of the original energy curve multiplied by eight.

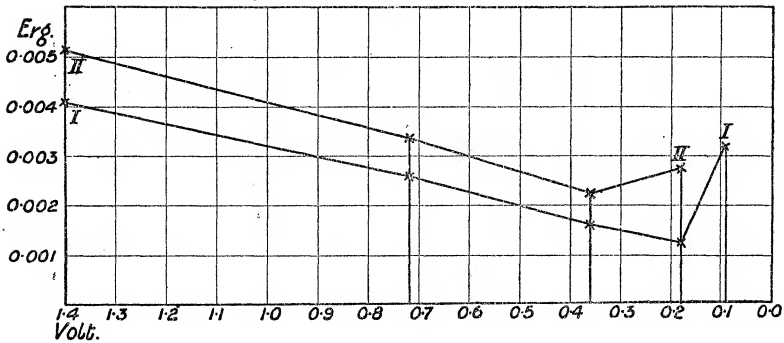
The second plan affords a rapid survey of the whole field of stimulation. When energy is varied by variation of voltage at any given capacity, it varies as voltage squared, and the constant of its curve is augmented directly as the voltage. The step from maximal to sub-minimal stimulation is comparatively large when we test at a series of diminishing voltages, and a voltage is soon reached at which no increase of capacity, however great, can bring out an effective stimulus, the constant of the energy curve being lowered as capacity is increased.

The third plan is useful only for closer determination of an optimum gradient, when the range within which it is to be sought for is approximately known. When energy is varied by variation of capacity at any given voltage, it varies directly as capacity, but the constant of its curve diminishes as capacity is increased, *i.e.*, a small increment of energy is obtained at a reduced gradient, as compared with a large increment of energy at a raised gradient obtained by increase of voltage.

Exp. 1.—Nerve-muscle Preparation. Resistance of Nerve + Electrodes  
= 150000  $\omega$ .

I	Capacity in micro- farads.	Pressure in volts.	Quantity in micro- coulombs.	Energy in ergs.	Con- stants.	Time of fall of energy to $\frac{1}{4}$ value.	Con- traction.
	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_3$ .	
Opt.	0·0004	1·44	0·000576	0·00415	{ 20850 2606	0·000042	small.
	0·0016	0·72	0·001152			0·000168	large.
	0·0010	0·72	0·00072	0·00259	{ 4170 521	0·000104	small.
	0·0040	0·36	0·00144			0·000416	large.
	0·0025	0·36	0·0009	0·00162	{ 834 104	0·000260	small.
	0·0100	0·18	0·0018			0·001040	large.
	0·0080	0·18	0·00144	0·00130	{ 130 16	0·000832	small.
	0·0320	0·09	0·00288			0·003328	none.
	0·0800	0·09	0·0072	0·00324	{ 6·5 0·8	0·008320	small.
	0·3200	0·045	0·0144			0·033280	none.
Fig. {	0·0400	0·09	0·0036	0·00159	{ 834 104 13	0·000260	none.
	0·0100	0·18	0·0018			0·001040	large.
	0·0025	0·36	0·0009			0·004160	small.

## Exp. 1.



The constant of the optimal minimal stimulus (*i.e.*, the characteristic) is 130. The energy falls to  $\frac{1}{4}$  of its original value in nearly  $\frac{1}{1000}$  sec.

The second portion of this experiment, although less typical than the first, exhibits a similar character. The minimal stimulus is higher and of higher gradient, but further experiments will be required before we may admit this latter change to be other than an accidental effect. In other experiments there has been diminution of minimal stimulus with lower gradient.

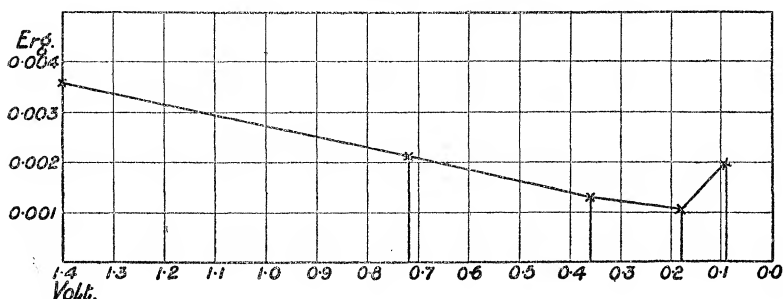
## Exp. 1 (repeated.)

II	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_{\frac{1}{2}}$ .	Con- traction.
Opt.	0.0005	1.44	0.000720	0.00518	{ 16680 2085	0.000052	small.
	0.0020	0.72	0.001440			0.000208	large.
	0.0013	0.72	0.000936	0.00337	{ 3210 401	0.000135	small.
	0.0052	0.36	0.001872			0.000540	large.
	0.0035	0.36	0.001260	0.00227	{ 596 74	0.000364	small.
	0.0140	0.18	0.002520			0.001456	none.
	0.0170	0.18	0.003060	0.00275	{ 61 8	0.001770	small.
	0.0680	0.09	0.006120			0.007080	none.
	0.0160	0.18	0.002880	0.00259	{ 4170 521 65	0.000104	small.
	0.0040	0.36	0.001440			0.000416	large.
	0.0010	0.72	0.000720			0.001664	none.

Exp. 2.—Frog. Sciatic Nerve.  $R = 80,000 \omega$ .\*

	Capacity in micro- farads.	Pressure in volts.	Quantity in micro- coulombs.	Energy in ergs.	Constant.	Time of fall of energy to $\frac{1}{2}$ of its original value. t.
	F.	V.	FV.	5FV <sup>2</sup> .	C.	sec.
Opt.	0·00035	1·44	0·000504	0·003629	44700	0·000019
	0·00085	0·72	0·000612	0·002203	9200	0·000047
	0·00200	0·36	0·000720	0·001296	1950	0·000111
	0·00700	0·18	0·001260	0·001134	279	0·000388
	0·05000	0·09	0·004500	0·002025	19	0·002770
No effect.	10·00000	0·045	0·450000	0·101250	0·05	0·554000
Opt.	0·0001	5·00	0·0005	0·012500	543000	0·000005
	0·0010	1·00	0·0010	0·005000	10850	0·000055
	0·0100	0·20	0·0020	0·002000	217	0·000554
	0·1000	0·10	0·0130	0·007450	14	0·005540
	1·0000	0·10	0·1000	0·050000	1	0·055400

## Exp. 2.



*Influence of Temperature.*—The characteristic of nerve is very sensitive to alterations of temperature, being raised by high temperature (30°), and depressed by low temperature (5°). Gotch and Macdonald have shown that stimulation of nerve by break induction shocks is favoured by heat, disparaged by cold, and that stimulation by the constant current is favoured by cold, disparaged by heat (13).† The present experiments show clearly that short stimuli (energy curve of high number) are

\* In the first group of trials given voltages are taken, and the minimum effective capacities sought for. The characteristic = 279.

In the second group given capacities are taken, and the minimum effective voltages sought for. The characteristic = 217.

† G. and M. allude to condenser excitation, but did not employ it correctly. They supposed that a "short" minimal stimulus could be obtained from a condenser of 0·5 microfarad.



effective at high temperature, ineffective at low temperature, while long stimuli (energy curve of low number) are effective at low temperature, ineffective at high temperature.

These results indicate further a point of probably considerable biological significance, inasmuch as the characteristic of frog's nerve at high temperature is found to approximate to that of mammalian nerve. Thus, whereas the characteristic of frog's nerve at room temperature (16° to 18°) is represented by a number of three digits, and that of human nerve at normal temperature (37°) by a number of five digits, the approximate characteristic (*i.e.*, the constant indicating the gradient of a suitable stimulus) of frog's nerve at high temperature (30°) is also expressed by a number of five digits. These and other data are tabulated in the concluding summary.

Exp. 3.—R = 70,000  $\omega$ .\*

T.	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_{\frac{1}{2}}$ .	
30°	0·0015	1·44	0·0022	0·015	11910	sec. 0·000073	{ Abolished by cooling. Abolished by warming.
5	0·5000	0·24	0·1200	0·139	6	0·024250	

For the first trial at 32° the voltage is taken at 1·44, and the minimum effective capacity is sought for and found to be a little below 0·0015.

In the second trial at 5°, the capacity is taken at 0·5, and the minimum effective voltage is sought for and found to be a little below 0·24.

The first or short stimulus is immediately rendered ineffective by cooling.

The second or long stimulus is immediately rendered ineffective by warming.

\* In experiments 3 and 4 the characteristic proper has not been determined, but only the constants of a short and long curve of minimal but not optimal minimal stimuli. An optimal minimal stimulus is rendered ineffective by heating and by cooling. The alterations of resistance by alterations of temperature have not been taken into calculation. Such alterations would, however, have only intensified the contrast already apparent between short and long stimuli, in accordance with the following numbers :—

T.	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_{\frac{1}{2}}$ .	R.
30°	0·0015	1·44	0·0022	0·015	16700	sec. 0·000052	50,000 $\omega$
5	0·5000	0·24	0·1200	0·139	4·17	0·034600	100,000 $\omega$
30°	0·0007	1·44	0·001	0·007	17900	0·000048	100,000 $\omega$
5	1·0000	0·09	0·090	0·040	0·391	0·139000	200,000 $\omega$

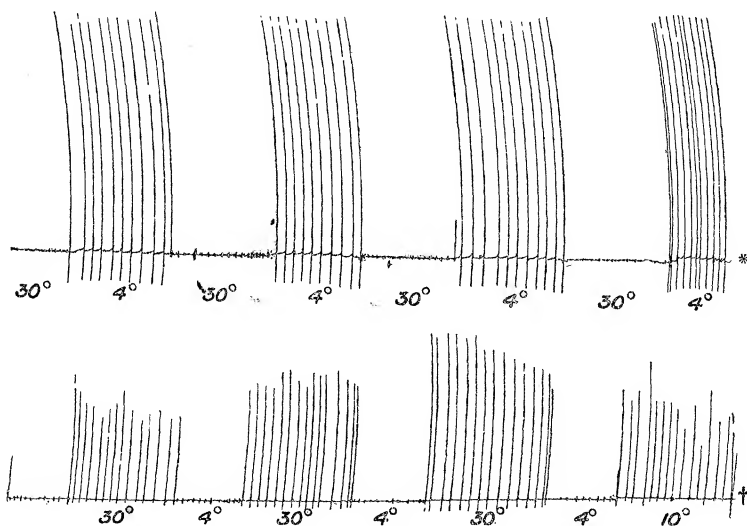
## Exp. 4.—Effects of High and Low Temperature upon Characteristic of Nerve.

$$R = 130000 \omega.$$

T.	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_{\frac{3}{4}}$ .	
30°	0·0007	1·44	0·001	0·007	11382	sec. 0·000063	{ Abolished by cooling. Abolished by warming.
4°	1·0000	0·09	0·090	0·040	0·6	0·090100	

Procedure similar to that of previous experiment.

The characteristic is raised by heat, lowered by cold, as in the previous experiment.



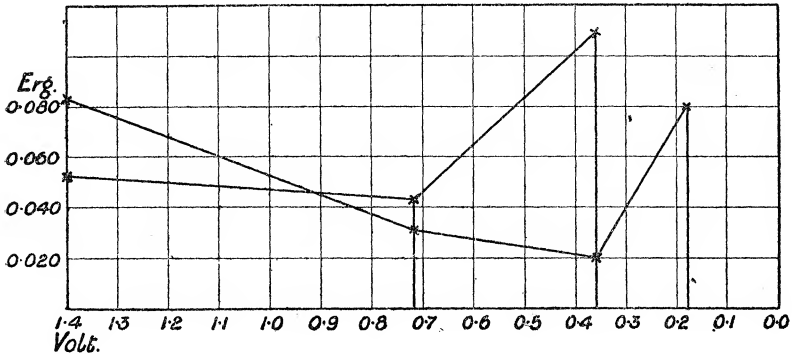
\* 1 microfarad, 0·09 volt.

† 0·0007 microfarad, 1·44 volt.

Exp. 5.—Cat. Sciatic Nerve. R = 17000  $\omega$ .

	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_3$ .
						sec.
Opt.	0·0022	2·88	0·0063	0·071	66910	0·000026
	0·0050	1·44	0·0072	0·052	14700	0·000059
	0·0170	0·72	0·0122	0·044	<b>2165</b>	0·000202
	0·1700	0·36	0·0612	0·110	108	0·002023
No effect {	0·5000	0·18	0·0900	0·081	18	0·005890
	1·0000	0·18	0·1800	0·162	9	0·011780
About 20 minutes later.						
Opt.	0·006	2·88	0·0173	0·249	24530	0·000071
	0·008	1·44	0·0115	0·083	9200	0·000094
	0·012	0·72	0·0086	0·031	3066	0·000141
	0·030	0·36	0·0108	0·019	<b>613</b>	0·000353
	0·500	0·18	0·0900	0·081	18	0·005890

Exp. 5.



The method of trial was to start with given voltage and find minimum effective capacities.

In the first group of trials the characteristic is 2165 ; in the second it is 613.

The constants of minimum effective stimuli at various voltages are higher in the first than in the second group.

Short stimuli are relatively more effective in the first group ; long stimuli in the second group.

Exp. 6.—Cat. Phrenic Nerve. R = 30000  $\omega$ .

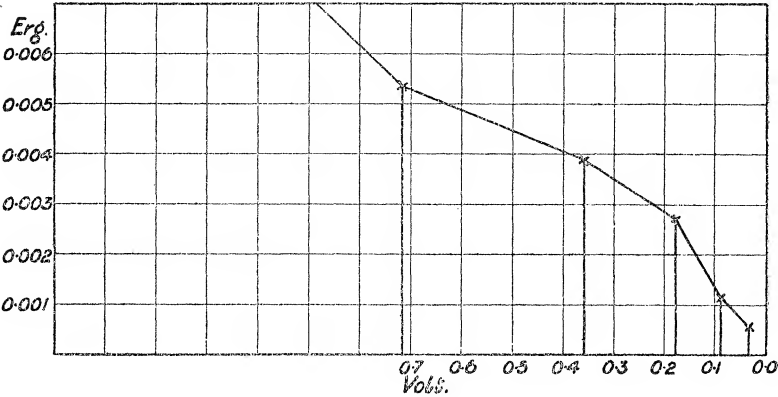
F.	V.	FV.	5 FV <sup>2</sup> .	C.	<i>t</i> <sub>3</sub> .
					sec.
0·0012	1·44	0·00173	0·012442	34700	0·000025
0·0021	0·72	0·00151	0·005443	9960	0·000044
0·0060	0·36	0·00216	0·003888	1740	0·000125
0·0170	0·18	0·00306	0·002754	307	0·000353
0·0300	0·09	0·00270	0·001215	87	0·000624
0·1000	0·036	0·00360	0·000648	10·4	0·002080

A few minutes later.

0·0085	1·44	0·01224	0·088128	4910	0·000177
0·6000	0·36	0·21600	0·388800	174	0·012500

Voltage given, capacity looked for.

Exp. 6.



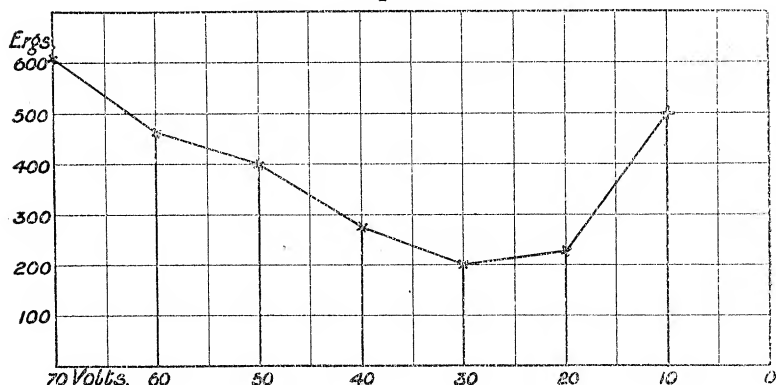
Exp. 7.—Man A. Ulnar Nerve. R = 12000.

	F.	V.	FV.	5 FV <sup>2</sup> .	C.	<i>t</i> <sub>3</sub> .
	mf.	volts.	mc.	ergs.		sec.
Opt.....	0·8000	10	8·00	400	905	0·006650
	0·1400	20	2·80	280	10350	0·001165
	0·0550	30	1·65	247·5	39500	0·000458
	0·0350	40	1·40	280	82500	0·000291
	0·0250	50	1·25	312·5	145000	0·000208
	0·0180	60	1·08	324	241500	0·000150
	0·0150	70	1·05	367·5	337500	0·000125

## Exp. 8.—Man B. Ulnar Nerve.

Opt.....	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_{\frac{1}{2}}$ .
	mf.	volts.	mc.	ergs.		sec.
	1.0000	10	10.00	500	725	0.008320
	0.1150	20	2.30	230	12600	0.000956
	0.0450	30	1.35	202.5	48250	0.000374
	0.0350	40	1.40	280	82500	0.000291
	0.0320	50	1.60	400	113000	0.000266
	0.0260	60	1.56	468	167000	0.000216
	0.0255	70	1.78	615	200000	0.000212

Exp. 8.

Exp. 9.—Man. Peroneal Nerve. R = 15,000  $\omega$ .

Opt.	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_{\frac{1}{2}}$ .	H.
	mf.	volts.	mc.	ergs.		sec.	mm.
	0.5000	20	10.00	1,000	2316	0.005200	0
	0.3200	25	8.00	"	4525	0.003330	trace
	0.2200	30	6.66	"	7825	0.002310	1.5
	0.1633	35	5.72	"	12400	0.001700	6.5
	0.1250	40	5.00	"	18530	0.001300	6.0
	0.0988	45	4.45	"	26375	0.0010300	4.5
	0.0800	50	4.00	"	36200	0.000832	4.0
	0.0661	55	3.64	"	48200	0.000687	3.0
	0.0556	60	3.34	"	62500	0.000578	2.5



25      30      35      40      45      50      55      60 volts.

.32      .22      .163      .125      .1      .08      .066      .055 mf.

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*Sensificatory Stimuli.*

In the attempt to determine a "characteristic" of various modes of sensificatory stimulation, I encountered the doubt, and, therefore, difficulty, inherent to all investigations where the experimental criterion is a subjective one—by appreciation of minimal sensation. This broad distinction was, however, clearly apparent, that whereas for series of stimuli of motor nerves the minimum exciting energy decreased to a minimum from which it rose again (diminishing voltage and increasing capacity), the energy of sensory stimuli of increasing duration decreased indefinitely towards a minimum value. Within the limits to which my experiments extended, decrease of energy was made up for by increase of its duration.

Testing on the human subject for minimal felt effect, by looking for minimum effective capacity at a series of given voltages, I found it difficult to distinguish between apparently different qualities of minimal sensation. In the case of cutaneous nerves, it was generally impossible to say whether the smallest "something felt" was directly cutaneous or directly subcutaneous, or indirectly subcutaneous, by

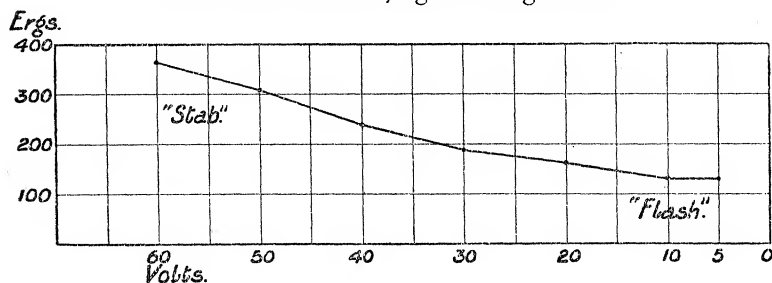
reason of some muscular contraction. In the case of the eye it was often difficult to tell whether the smallest "something felt" were a slight common sensation or a slight photophene.

In the case of the eye this point, however, came out with satisfactory distinctness, viz., that low in the energy series, *i.e.*, with longer stimuli by lower voltage at greater capacity, the subject of experiment is more conscious of a "flash" (optical sensation) than of a "stab" (common sensation), whereas high in the energy series, viz., with shorter stimuli by higher voltage at lower capacity, the subject feels a "stab" (common sensation) more readily than a "flash" (optical sensation). This indicates that longer stimuli are better adjusted to the excitability of the retina, shorter stimuli to the excitability of common sensory terminal organs.

Eyeball.  $R = 12000$  ohms.

	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t\frac{1}{2}$ .
Pain.....	0·020	60	1·2	360	217000	0·000166
	0·025	50	1·25	312·5	145000	0·000208
	0·030	40	1·2	240	96500	0·000250
	0·040	30	1·2	180	54300	0·000333
Flash.....	0·080	20	1·6	160	18100	0·000665
	0·250	10	2·5	125	2900	0·002030
	1	5	5·0	125	362	0·008320
Pain.....	0·015	60	0·9	270	290000	0·000125
	0·020	50	1·0	250	181000	0·000166
	0·030	40	1·2	240	96500	0·000250
	0·040	30	1·2	180	54300	0·000333
Flash.....	0·060	20	1·2	120	24100	0·000499
	0·200	10	2·0	100	3620	0·001660
	0·500	5	2·5	62·5	724	0·004160

Pain to short stimuli, light to long stimuli.



This principal conclusion is confirmed by experiments conducted on the first plan of procedure, viz., by testing with stimuli of equal energy

at various gradients. To this end I found it convenient to first settle upon a minimal sensation at a given mean voltage, and then to make two further trials, one at half the voltage and four times the capacity, the other at double the voltage and one-fourth the capacity. Each group of three tests was thus at the same energy, but with the constants of the three discharge curves in the proportion 1, 8, 64. The minimal sensation having been settled with the constant at 8, it could be inferred from equality or inequality of the effects at higher and lower constants, whether the constant of a fitting stimulus lay above or below either of the two extremes.

	F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_3$ .	Sensation.
Forearm, common sensation. R = 45000	0.4000	12	4.8	ergs. 288	579	0.001250	None.
	0.1000	24	2.4	288	4632	0.000313	Slight.
	0.0250	48	1.2	288	34056	0.000078	Marked.
Tongue, common sensation. R = 7500	0.0800	12	0.96	57.6	17380	0.000416	Marked.
	0.0200	24	0.48	57.6	139040	0.000104	Slight.
	0.0050	48	0.24	57.6	1112320	0.000028	None.
Optical sensation. R = 21000	0.2400	12	2.88	172.8	2031	0.003493	Marked.
	0.0600	24	1.44	172.8	16248	0.000873	Slight.
	0.0150	48	0.72	172.8	129984	0.000218	None.
Movement, median nerve. R = 30000	0.2000	12	2.4	144	1706	0.004158	(Movement). None.
	0.0500	24	1.2	144	13648	0.001040	Slight.
	0.0125	48	0.6	144	109184	0.000280	None.

To verify the statement that at equal energy retinal stimulation predominates when the gradient is low, and common sensory stimulation when the gradient is high, it is preferable to take stimuli above the minimal and with larger difference of gradient, as *e.g.*, in the following experiment:—

Anode on Eyeball. Kathode on Abdomen. R = 9000 ohms.

F.	V.	FV.	5FV <sup>2</sup> .	C.	$t_3$ .	Sensation.
mf.	volts.	mc.	ergs.		sec.	
0.04	54	2.16	583.2	130200	0.000250	Stab only.
0.36	18	6.48	583.2	4828	0.002245	Stab + flash.
3.24	6	19.44	583.2	179	0.020200	Flash only.